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Bibliography

- ARDEN, G. B., and TANSLEY, K. (1955): The spectral sensitivity of the pure-cone retina of the grey squirrel (Sciurus carolinensis leucotis). Journal of Physiology 127:592-602.
 KOLOSVARY, C. A. (1934): A study of color vision in the mouse (Mus musculus) and the sous-lik (Citellus citellus L.). Journal of Genetic Psychology 44:473-477.
 LOCHER, CHARLOTTE J. S. (1933): Untersuchungen über den Farbensinn vom Eichhörnchen.
- Leiden, Brill, 56 p.
- REIMOV, R. (1957): An experimental study of the color vision of the dwarf souslik (Citellus pygmaeus Pall.) in the field. Academy of Sciences, USSR, Proceedings, Biological Science Section 114:585-587. May-June 1957. (Trans. by American Institute of Biological Sciences).
- TINBERGEN, NIKO (1951): The study of instinct. Oxford, Clarendon Press, 228 p.
- WALLS, G. L. (1942): The vertebrate eye and its adaptive radiation. Bloomfield Hills, Cranbrook Press. 785 p. (Cranbrook Institute of Science Bulletin No. 19).

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Observations on the internal Structure of the Aorta in East African Mammals, with particular Reference to the Klipspringer, Gerenuk and Hippopotamus

BV SYLVIA K. SIKES

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Introduction

During a recent field survey of cardiovascular disease in free-living wild mammals and birds in East Africa¹ a technique was developed for the comparative estimation of lipoidal and calcific deposits in the arterial wall in mammals. As a result of the consistent use of this technique throughout the survey, some peculiarities of structure of the aortae of certain species were noted.

The most outstanding of these were found in the klipspringer (Oreotragus oreotragus Neumann), the gerenuk (Litocranius walleri Brooke), and the hippopotamus (Hippopotamus amphibius Heller). It is possible that these specialisations of structure may have a functional relationship to the habits of the species concerned.

Materials and Methods

1. Collection of specimens

Specimens of free-living wild mammals were selected and shot in East Africa by the author, with the specific purpose of examining the cardiovascular system. To ensure minimal damage to the circulatory system, they were usually killed by means

¹ Financed by the British Heart Foundation, and carried out under the auspices of the Zoological Society of London.

of a solid rifle bullet fired into the central nervous system, so that death was instantaneous. On-site autopsy was carried out immediately with the minimum disturbance of the carcass. A wide range of ecological reference data, tissue, and parasite samples was also collected from each animal in connection with the pathological side of the survey.

2. The need for a consistent technique

The survey included mammals which ranged in size from the mole-rat (*Cryptomys* sp.) to the elephant (*Loxodonta africana*). Existing techniques, as generally used in medicine and veterinary pathology, were not practicable in the case of very large mammals such as hippopotamus, rhinoceros, and elephant. Previously it was customary in the case of very large mammals merely to cut samples of the aortae of such species for pathological examination rather than the whole aortae. In this project, however, it was soon apparent that a consistent field and laboratory technique, in which the whole aorta of each species could be examined, would be more valuable if intra-aortic disease patterns were to be studied on a comparative basis. Moreover, systematic comparative studies of the normal internal structure of the arteries of free-living wild animals (as distinct from captive) did not appear to have been attempted previously.

A considerable body of data is available on the internal, especially the microscopic, anatomy of certain species of domestic, captive, and experimental animals (GILLMAN 1964; BERTELSEN 1963; BUCK 1963; FRENCH 1964), but most of this is related to arterial pathology, rather than the normal structure (GILLMAN 1964). Even in the

o r c c

anterior (cranial)

posterior (caudal)

Fig. 1 a (lefl). Internal surface of aorta of hippopotamus. Portion 1 (anterior), dorsal quarter — Fig. 1 b (right). As above, Portion II, dorsal quarter. — b supportive band, c = ostial collar, d = depression of ostium, o — ostium, r = ostial ramp case of man, published descriptions of the details of the normal supportive structures of the arterial wall have been surprisingly few. Even the terms suggested by the various authors to describe these structures were found to be inadequate in this survey for purposes of distinguishing the different types. For example, CONTI (1953) called them "cushions of smooth muscle and elastic fibres". STEHBENS (1960) described them as "intimal pads", and FINLAYSON (1965) as "supportive thickenings". Others however, have thought them to be pathological or traumatic (SODE-MAN 1961; THURLBECK 1965).

It was therefore found necessary not only to use a standardised technique for the examination of the internal structure of the aortae on a comparative basis, but also to coin new terms for describing the different types of arterial supportive structures noted, namely: "ostial collars", "ramps", and "ridges"; and "supportive bands" and "threads".

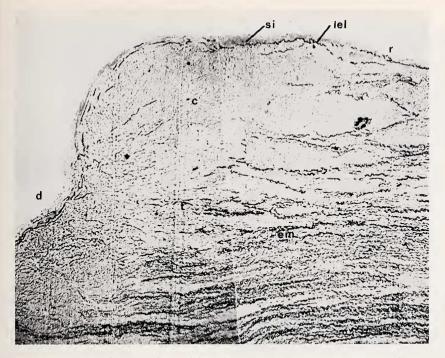


Fig. 1c. L. S. ostial collar of dorsal branch artery originating in Portion I of aorta of hippopotamus. Sudanophilic lipid deposits are located in the *tunica intima* overlying the collar. The elastic lamellae of the *tunica media* (heavily stained) terminate at the collar and are replaced by crescentically orientated smooth muscle cells and collagen fibres. The internal elastic lamella is also re-orientated at the collar into alignment with the underlying fibro-elastic crescent. -c = ostial collar, d = depression of ostium, em = elastic lamellae of *tunica media* (heavily stained), iel = internal elastic lamella, r = ostial ramp, si = sudanophilic lipid deposits in *tunica intima* of ostial collar, t = termination of elastic lamellae of *tunica media* a tostium

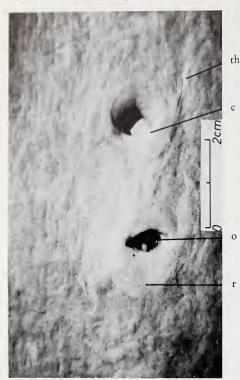
The ostial collar is the collar-like thickening containing abundant smooth-muscle cells and elastic fibres crescentically arranged distal to the ostial depression or funnel of smaller branch arteries. In the rim of these collars the *tunica intima* as well as the *tunica media* is usually slightly thicker than elsewhere. The "ramp" is a triangular extension of the collar, distal to it. Here, the smooth-muscle cells and elastic fibres are orientated in the longitudinal line of the aorta. Sudanophilic lipid deposits usually occur within the ostial depression and in the intima of the ramp (Fig. 1 [a] and [b]; 2 [a]).

"Ostial ridges" are the supportive ridges characteristically found in the crutch of an arterial bifurcation and, like the other supportive structures, are rich in elastic fibres and smooth-muscle cells (Fig. 2 [b]).

"Supportive bands and threads" consist of various supportive thickenings of the arterial wall either linking neighbouring ostia, or arranged in a fan-like or parallel pattern through the arterial intima and media in lines along which mechanical stresses operate on the arterial wall: for example, in Portion I (anterior) of the thoracic aorta where extreme changes in haemodynamic pressure may be set up, for instance, after prolonged or sudden exercise; or in the region of the origins of the coeliac, anterior mesenteric and renal arteries, where there may be active haemodynamic turbulence.

These supportive structures are usually readily detectable with the naked eye or a

anterior (cranial)



posterior (caudal)

Fig. 2 a. Internal surface of Portion I (anterior), dorsal quarter, of aorta of an elderly bull elephant -c = ostial collar, o = ostium, r = ostial ramp, th = supportive thread

distal

proximal

Fig. 2 b. Internal surface of the brachial artery of the same elephant, showing the supportive ridges; with fairly heavy intimal, sudanophilic lipid deposits overlying, and confined to, the area of the supportive ridges. There is no evidence of any pathological lesions in this artery. The ostial collar of a minor branch artery is indicated — c = ostial collar, rd =supportive ridge

hand lens as rather pale, somewhat raised structures in the larger mammals, but have apparently sometimes been confused in smaller mammals with the fatty lesions of atheroma. The distinction between fatty lesions and these normal structures can really only be made unequivocally by means of gross-staining tests and frozen-section microscopy.

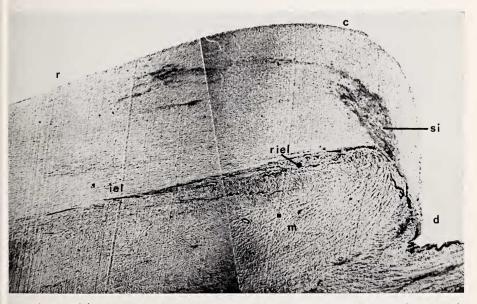
3. Techniques used for the field treatment of the arteries of large and small mammals

Immediately after death, and the taking of measurements, the carcass was rolled on to its right side (larger mammals) if possible, or on to the dorsum (smaller mammals). The body wall of the left side was removed and the internal organs pressed carefully down and away from the dorsal line with the hand, separating them from the aorta. This exposed almost the entire length of the aorta from the arch to the bifurcation. The aortic arch and thoracic aorta were freed *in situ* from any connective tissue. The length of the aorta was measured and its position and proportion noted.

The dorsal aorta was then severed from the aortic arch by a transverse incision running through the scar of the *ductus arteriosus*, carefully separated from any remaining connective tissue, and removed from the carcass. Care was necessary to avoid stretching, twisting, or compressing the aorta lest the very delicate intima should be damaged.

The separated aorta was placed in a vessel containing water, and rinsed carefully, before tidying away fat and connective tissue adherent to the adventitia. The aorta was then laid on a dissecting board or dish and slit longitudinally with blunt-ended scissors along its mid-ventral line. It should be noted that the orientation of the aorta is described here relative to the body of the adult animal, not to its embryological or evolutionary origins. It was then laid on a stiff polythene board, or boards (3 mm thickness for larger animals – e. g. size-range gazelles or jackals to elephants; 1.5 mm thick for animal smaller than gazelles and jackals). A convenient size of board was 8 ins \times 10 ins (20 cm \times 20 cm), as these could later be stacked on edge in tanks of preservative.

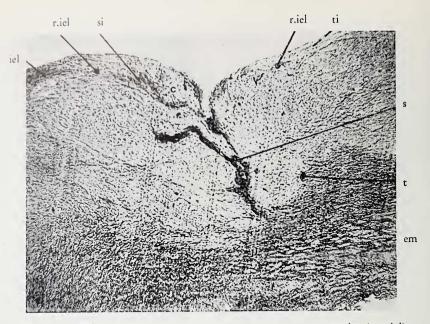
If larger than the board, the aorta was apportioned by cutting it transversely into convenient lengths and mounting these in linear order on separate, numbered boards. The aorta (or its separate portions) was then opened out, — with the intimal surface uppermost, and stapled to the board with a long-arm stapler using stainless steel staples. Care was necessary to avoid touching or 'stroking' along the internal surface of the aorta with the fingers or any instrument, as this would damage the intima. The mounted aorta, (or the portions of the aorta) was then rinsed with clean water or saline before putting each mount into a perforated, protective polythene bag, and stacking the packages standing on edge in a tank of $10^{\circ}/_{\circ}$ formol-saline. Arteries, and samples of arteries, other than the aorta, were treated by exactly the same technique.



posterior (caudal)

anterior (cranial)

Fig. 3a. L. S. of ostial collar and part of ramp distal to a dorsal ostium originating in Portion II of the aorta of an elephant. Both the media and the intima are thick in this locality, and contain abundant smooth muscle and collagen fibres. Small deposits of sudanophilic lipids occur in the intima of the collar, overlying the point of re-orientation of the internal elastic lamella. — c = ostial collar, d = depression of ostium, iel = internal elastic lamella, m = tunica media, r = ostial ramp, r.iel = point of re-orientation of internal elastic lamella, si = sudanophilic lipid deposits in tunica intima of ostial collar



posterior (caudal)

anterior (cranial)

Fig. 3b. L. S. cut along the lateral rim of the ostium of the aorta of a hippopotamus, showing the deposition of sudanophilic lipid both in the intima of the ostial collar, and in the media of the ostial depression. Points of re-orientation of the internal elastic lamella are visible both anterior and posterior to the ostial depression; the thickened fibro-muscular collar, however, lying only posterior to it. — em = elastic lamellae of *tunica media*, iel = internal elastic lamella, riel = point of re-orientation of internal elastic lamella, s = sudaophilic lipids deep in ostium, si = sudaophilic lipid deposits in *tunica intima* of ostial collar, t = termination of elastic lamellae of *tunica media* at ostium, ti = *tunica intima*

4. Laboratory examination of the aortae

The preserved aortae were examined in the laboratory a. without further treatment; b. gross-stained with Sudan IV stain; c. by radiography; and d. by light microscopy using both stained frozen sections and stained paraffin sections.

a. Where the aortae had been mounted in separate portions, these were first reassembled in order. Accurate scale drawings were made of each aorta and the drawings apportioned for analysis. Taking the transverse line through the scar of the *ductus arteriosus* as the anterior base line, and the bifurcation as the posterior limit of the aorta, the length was divided into five equal portions. Each of these was then quartered longitudinally into four comparable portions, namely the dorsal, right lateral, ventral (actually represented by two pieces V_1 and V_2 , because the longitudinal incision was made along the mid-ventral line of the aorta), and left lateral.

It was necessary to apportion the aorta in this way to allow for differential contraction of the aorta in length and width following removal from the carcass. In ideal field conditions, previous perfusion and fixing of the aorta *in situ* might be preferable, but would be disadvantageous for the subsequent examination of the intimal surface itself. If left *in situ* for more than about one hour in warm temperatures, decomposition of the intima occurs, so any possible advantage gained by loss of elasticity would be disadvantageous for the examination of the *tunica intima*. It should be noted that it is not always possible to distinguish lesions in the intima from the normal supportive thickenings with the naked eye or a hand-lens. Further treatment is essential for the interpretation of these. Fig. 4 shows the apportionment of the scale drawing of the aorta of a Cape buffalo (Syncerus caffer Caffer Sparrman).

b. Gross staining with Sudan IV was used according to HOLMAN'S method (HOL-MAN et al. 1958). Each complete mount, including the polythene board, was immersed in the staining solutions. Agitation of the mount was necessary at intervals to ensure even penetration by the stain. The presence of both normal and pathological deposits of sudanophilic lipids in the intima was clearly demonstrated by this method, but they were not distinguishable from each other. The stained areas were drawn accurately on the scale drawings (see [a], above) by means of a mechanical drawing instrument, and their distribution determined by means of area counts using a 5 mm grid.

To provide comparable figures for aortae of all sizes and age groups within each species, the ratio of the area of aorta wall containing lipid deposits to the area of the portion of aorta wall estimated was determined. An alternative method was the use of percentages. In the case of the African elephant, (on whose aortae more extensive studies were carried out: SIKES 1967) intra-aortic lipid distribution was also represented graphically by means of histograms.

c. Radiographic techniques were used to investigate intra-aortic calcium distribution. Each mounted aorta, or portion of aorta, was laid on top of a radio-opaque grid of 5 mm squares marked on a thin perspex sheet, and radiographed by means of a Watson Dental X-ray unit. Quantitative counts of the area of each portion of the aorta wall were made in the same way as for the lipid distribution, except that the need to make scale drawings was eliminated by the inclusion of the grid in the radiographs. Direct counts on the viewer could therefore be made.

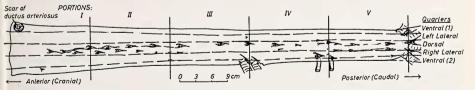


Fig. 4. Cape Buffalo. Internal surface of Aorta

d. Microscopic examination. For the detailed investigation of sudanophilic lipid distribution, thick frozen sections (5–8 μ) were cut, and stained with Sudan IV and haemalum. It was found that, while the Sudan IV gross-staining technique was adequate for the demonstration of intimal lipid deposits, frozen sections were essential if medial lipid deposits were also to be detected. Normal paraffin-section and staining techniques for histology were also used for the examination of sets of tissue slips cut from standardised positions in each aorta.

Internal Anatomy of the Aorta Distal to the Ductus Arteriosus

1. Arrangement of branch arteries and the aortic bifurcation

Figures 4 to 8 illustrate, by means of scale drawings, the arrangement of branch arteries und supportive thickenings in the aortae of nine species belonging to the orders Artiodactyla, Perissodictyla and Proboscidea. All are members of the East African fauna and were collected and treated in the field and laboratory by the techniques outlined above.

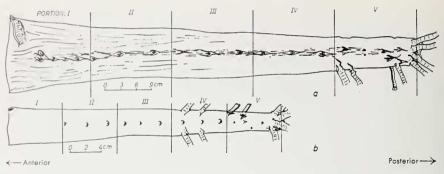


Fig. 5 a. Hippopotamus - b. Warthog

Although some degree of intra-specific individual variation exists in the arrangement of the ostia of the paired dorsal branch arteries, and in the position of origin of the unpaired visceral arteries (coeliac, anterior mesenteric, spermatic and ovarian; and the arteries originating at or near the bifurcation), a basic pattern characteristic of each species could be recognised.

In Fig. 7, the internal anatomy of the aorta of the African elephant is illustrated at various stages of growth by means of scale drawings. Individual congenital variants have been represented in drawings (b) - (e), while the commonest arrangement is illustrated in drawing (a). The variants illustrated include the case of a caudal artery originating at the bifurcation between the common iliac arteries (b); renal arteries with a common origin (c); the common origins of dorsal paired arteries in portion I (anterior) (d), and the coeliac and anterior mesenteric arteries with a common origin (e).

In spite of these intraspecific variations, however, the general proportions of the aorta were found to remain remarkably constant even at different ages. It was noticeable, however, that the ostial collars, ramps and ridges as well as the supportive bands and threads become increasingly prominent with increasing age. In very elderly animals the supportive threads may become so prominent that they give the intimal surface a "wrinkled" appearance. This, however, is to be distinguished from the honeycomb appearance typical of the disease of *medial sclerosis* in elephant (SIKES, in press [a]).

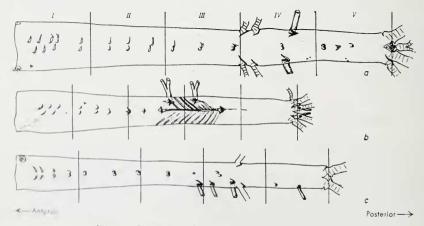


Fig. 6 a. Gerenuk - b. Klipspringer - c. Steinbok

The arrangement and proportions of the branches of the aorta of the African elephant (Loxodonta africana) were found to differ little from those of the aorta of the African Cape buffalo (Syncerus caffer caffer) (Fig. 4) and many of the larger antelopes of the non-arid African savannah. They differ radically, however, from the arrangement seen in the aorta of the hippopotamus (Hippopotamus amphibius) (Fig. 5), in which the origins of the coeliac, anterior mesenteric and renal arteries are all located in the posterior fifth of the aorta.

Although the hippo is taxonomically frequently included with the warthog (*Phacochoerus aethiopicus*) in the sub-order *Suiformes*, its aorta does not appear to resemble that of the warthog in the arrangement either of its branch arteries or of its supportive thickenings. Indeed, the reduced number of dorsal ostia and the tendency

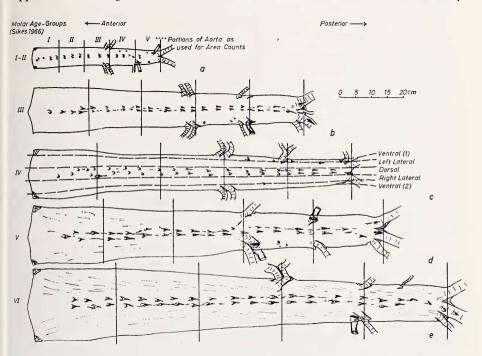


Fig. 7. African Elephant. Normal Aorta: at successive stages of growth (Internal surface). Some common minor variations in structure are shown.

for all paired dorsal arteries to share single ostia, differs from the arrangement in other East African ungulates examined by the author.

In the rhinoceros (*Diceros bicornis*), not only are the origins of the coeliac, anterior mesenteric, and renal arteries located further forward in the aorta, in portions III and IV, but they are also more evenly separated from each other (Fig. 8). In this species, the arrangement at the bifurcation is exceedingly complex and apparently very variable. Moreover, the internal surface of the rhinoceros aorta even in younger animals is characterised by its very prominent pattern of supportive threads and bands, the ostia of the paired dorsal arteries being set in an elaborate and characteristic arrangement of ostial collars and ramps.

In contrast to the rhinoceros, the aorta of the zebra (*Equus burchelli*) – the only other perissodactyl examined here (Fig. 8) – even in the case of elderly stallions, was found rarely to have a prominent aortic pattern of supportive thickenings, the ostia

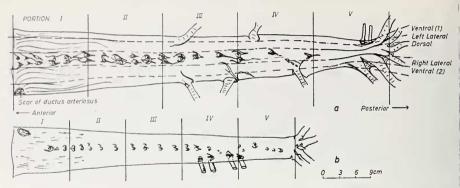


Fig. 8. Above: Rhinoceros. Aorta, internal surface (Young adult animal), Below: Zebra

of the paired dorsal arteries being generally somewhat rounded, and lacking either distinctive ostial ramps or a dorsal supportive band.

The most striking features of the internal anatomy of aortae of the East African mammals examined were those found in four species, which either stand naturally with the dorsum sloping downward towards the quarters, or which tend to assume a vertical position for long periods when feeding. The giraffe (*Giraffa camelopardalis*), gerenuk (*Litocranius walleri*), klipspringer (*Oreotragus oreotragus*) and the steinbok (*Raphicerus campestris*), all showed a distinctive, and characteristic, cup-shaped structure of the ostial collars of the dorsal branch arteries. The ostial collars in these species tended to be greater in width than length, where "length" refers to the direction of the longitudinal axis of the aorta. There was also a tendency for the anterior ostial collars to be slanted diagonally across the longitudinal axis of the aorta; this was most pronounced in the klipspringer (Fig. 6).

The most remarkable of the aortae of these four artiodactyls was that of the klipspringer. A regular, and very clearly defined, arrangement of parallel fibrous ridges passes digonally from a dorsal, longitudinal ridge to the left and anteriorly, around the lumen of the aorta, across the ventral line, to become reduced in prominence and disappear just before reaching the dorsal line again. The whole structure may act as a valve and serve to create an anticlockwise vortex in the region of the main aortic visceral branches. The apparatus lies in the portion of the aorta containing the common origins of the coeliac and anterior mesenteric and the two renal arteries.

Other striking deviations from the usual anatomy of the aortae of savannah antelope and gazelle are the absence of ostia of branch arteries in the abdominal aorta between the renal arteries and the bifurcation, and the extreme prominence of the supportive ridges at the bifurcation.

The peculiar anatomy of this aorta may have a functional explanation in terms of the specialised habits of the klipspringer. It is a chamois-like rock dweller (FRECHKOP 1955), frequently reported at altitudes of up to 9,000 ft. in East Africa, and occurring throughout the mountainous regions and rocky outcrops of Africa south of the Sahara, although nowadays apparently it is nowhere common. It makes vast leaps from rock to rock and frequently adopts a vertical posture when feeding. FRECHKOP (1955) wrote: "It can clearly be distinguished from all other antelopes by the way it stands only on the anterior rim of its hooves, and by the entirely different character of its pelage, and must therefore at present be regarded as belonging to a distinct subfamily, the Oreotraginae Pocock, 1910." GRASSÉ, in his "Traité de Zoologie" (1955) provisionally assigned it to this sub-family.

No reference to the aortic valve-like anatomy described above could be located

in the literature. The habits of the klipspringer were described by LYDDEKER (1926). COUTURIER (1938) described the heart and blood composition of the chamois, but made no reference to aortic structure. It is thus only possible at this stage to suggest that this apparatus may function as a blood-control mechanism, whereby, during undisturbed periods of browsing and/or rest, more blood is passed to the viscera and less to the hind limbs; then, when fear and the sudden demands for the physical activity of rapid escape over the rocks occur, the aorta is dilated (or perhaps the valve ridges relaxed), allowing the main volume of blood in the aorta to pass uninterrupted to the posterior vessels at the bifurcation, and thence to the hind limbs. If this hypothesis is correct, and the mechanism in the chamois is similar, it may in part explain the extraordinary range of fluctuation of heartbeat rate COUTURIER (1938) found in that species: namely from 80–200 beats per minute.

Much more detailed study of the flow of blood within the aorta and of the distribution of nerves to this aortic valve-like apparatus would be necessary to confirm this hypothesis. Nevertheless, it is certainly to be supposed that such a peculiar and specialised anatomical arrangement within the aorta has a functional relationship to the specialised habitat and mode of life of the species.

As a result of the comparative approach to the study of the internal anatomy of the aortae of mammalian species examined by the technique described above, it was apparent that the supportive structures and the general arrangement of branch arteries were not constant among species belonging to taxonomically related groups, but seemed rather to bear a relationship to the habits of the species.

Thus, the aortae of level-backed ungulates and sub-ungulates, as well as carnivores, living in non-arid savannah were seen to be generally similar. The rupicolous and sloping-backed species examined were found to have cusp-like ostial collars on the distal side of the origins of branch arteries, and prominent reinforcing ridges at the bifurcation. In addition, arid-, and semi-arid, adapted animals, such as the gerenuk (SCHOMBER 1966), showed a tendency to have a reduction in the number of branches originating directly in the aorta. The warthog, which tends to assume a forwardsloping stance when kneeling to rootle, was found to have a reduction in the number of branches originating directly in the thoracic aorta. In contrast, the steinbok, gerenuk and klipspringer, which tend to adopt a vertical stance when feeding, were found to have a reduction in the number of branches originating directly in the number of branches originating directly of branches originating directly in the adopt a vertical stance when feeding, were found to have a reduction in the number of branches originating directly in the abdominal aorta.

The hippopotamus, in which the haemodynamics may be supposed to be specifically adapted to the amphibious habit (GRATIOLET 1860; SCHOLANDER 1965) was found to have an arrangement of the aortic supportive structures more complex than was seen in any of the other 42 species of East African terrestrial mammals whose aortae were examined by the author. In the hippopotamus, the structure of each ostium differs recognisably from that of elephant and buffalo (Fig. 1 and 5) and the fibro-elastic collars and reinforcement ramps are very pronounced. In older animals, they unite in the dorsal line to form a characteristic, longitudinal band of raised and sometimes roughened tissues. A great deal of variation in number and arrangement of the ostia was noticed, and, in both the thoracic and abdominal portions, these may be either distinctly paired or apparently single. Close examination of the fibrous collars of the single ostia, however, suggested an early (perhaps intra-uterine) fusion of the pair to form a common orifice (Fig. 5).

Other features, which seem to be characteristic of the normal hippo aorta, included: I. the unusually large proportion of smooth muscle in the *tunica media* throughout the aorta; II. the organisation of this to form numerous, thin, longitudinal fibromuscular bands and threads, lying in the thoracic aorta just below the internal elastic lamella, and fanning from a focus in the dorsal aspect of the aortic arch, at the level of the *ductus arteriosus* in a general posterior direction. These were particularly clearly defined in the thoracic aorta of the full-term foetus and in all other specimens give the intimal surface a distinctive longitudinal pattern. In the two oldest specimens, this patterning was also wavy and rough and recalled (although not so advanced) the condition seen in an elderly male elephant (Fig. 2, SIKES, in press [a]). In the abdominal portion of the aorta of these elderly hippos, the pattern appeared to be predominantly transverse in direction, fanning from the origins of the larger branch arteries and bifurcation.

This characteristic arrangement of unusually elaborate and prominent fibro-muscular collars, ramps, ridges, bands and threads associated with all branch-artery ostia, and in particular those of the dorsal line, would seem to suggest a particular adaptation to the natural habits and environment of the hippopotamus. Perhaps the ostial 'collars' are able to exert some control over the size of the ostium. It would seem also that the hippo aorta is not only exceptionally elastic, but also contains an unusually high proportion of smooth muscle, suggesting that perhaps the aorta itself is developed to an unusual extent as a self-adjusting blood-pressure control mechanism adapted to periods of prolonged or deep submersion under water. Little is as yet known about the physiology of the circulatory system of the hippo during the periods of submersion, which are said to average anything from 20 seconds to 4–5 minutes, but may well be longer (FRECHKOP, 1955). VERHEYEN (1954) described a supposed controlling muscular sphincter in the vena cava at the level of the diaphragm in hippo, analogous to that in the seal.

One gains the impression that the normal hippo aorta possesses several specialised adaptations to its amphibious habit which would reward further study. Some of the features described by previous workers as degenerative changes (THURLBECK, 1965) would appear, when examined in comparison with the normal arterial supportive structures seen in other large mammals, such as elephant and buffalo, also to be normal structures, exhibiting, however, an exceptional degree of prominence associated with their adaptive specialisation.

2. Functional anatomy of the ostia and supportive structures

It has frequently bee assumed in the past in human veterinary pathology that the presence of lipid deposits in the tunica intima of the elastic and muscular arteries denoted an abnormality. Diffuse lipid deposits, described as 'fatty streaks', and the more complicated deposits known as 'atheromatous buttons' and 'plaques' have been regarded as early stages in the pathogenesis of atherosclerosis, which in man is frequently associated with thrombosis, and, where it affects the coronary arteries, with terminal cardiac failure (MCGILL & GEER, 1963). The histopathology of such lesions has been very fully described in the literature of medicine and comparative medicine (BRANWOOD, 1963; SANDLER & BOURNE, 1963; ROBERTS & STRAUS, 1965). Frequent comment, however, on the occurrence of lipid deposits in the tunica intima of the arteries of infants and young children has also been made (MCGILL & GEER, 1963; GONZALEZ, 1963) and a very detailed study of their chemical character in all age groups in man by SMITH et al. (1967). Recent research in comparative medicine suggests that some of these lipid accumulations may represent periodic events in a normal physiological process (THORP, 1963; BOYD, 1963; LIKAR et al. 1965). In the present survey, small intimal lipid deposits were detected in certain locations in the arteries in almost every mammalian specimen examined. The few exceptions included very small mammals, where there was a possibility that the gross-staining technique was insufficiently sensitive to detect the minute quantities of lipid present. They also included a few larger specimens, in which some delay had occurred, and decomposition had set in, before the aorta and samples of other arteries could be dissected from the carcass.

The normality of such deposits was investigated quantitatively in elephants to see if arterial lipid deposition was in any way habitat-related. It was found that the presence of small, uncomplicated arterial lipid deposits occurred universally in elephant in all habitats including that treated as the 'natural' type, or norm, namely unrestricted montane indigenous forest and alpine moorland (SIKES, in press, [a] and [b]). In all cases of this type the lipid deposits were confined to the areas of the arterial *tunica intima* overlying the supportive collars, ramps, ridges, bands and threads, and could not be located elsewhere.

In calves and lactating and/or pregnant cows, these uncomplicated arterial lipid deposits were greater in quantity than in other mature healthy elephants, suggesting a direct relationship to changes in lipid metabolism associated with milk production and milk consumption. No arterial lipid deposits were found in a full-term elephant foetus.

In elephants living in overcrowded conditions in the "stressed" ecosystems of "degenerate", or ecologically "disturbed" habitats, heavy deposits of arterial lipid were found in some older animals of both sexes (SIKES, in press [b]). These heavy deposits were associated with fibrous hyperplasia of the intima, disruption of the internal elastic lamina, hyaline degeneration of the *tunica intima*, and some metaplastic changes including, in very advanced cases, calcification of the intima. These changes in the intima resembled lesions characteristic of atheroma in man, and similarly were apparently irreversible and pathological (FRENCH, 1964; OGILVIE, 1962).

Reviewing the situation in the other free-living wild species of mammals collected and examined in their natural habitat-range, it seemed most probable that the presence of small, uncomplicated intimal lipid deposits associated with the arterial supportive structures is a normal, reversible physiological occurrence. Spontaneous reversibility of the lipid component in certain types of human plaque, generally referred to as atheromata up to the present, was described by KATZ & PICK (1963), and the known reversibility of fatty streaking in infants and young people, rabbits and chicks discussed, but the authors did not indicate whether these might really be regarded as part of a normal physiological process. If this is the case, it seems probable that these localised reversible lipid deposits may be functionally important to the supportive structures. (SMITH et al. 1967).

If, as suggested by the elaborate anatomical specialisation of these structures in the klipspringer and the hippopotamus, for example, they function as a mechanism controlling blood flow into the ostia of the smaller branch arteries from the aorta and larger muscular arteries, the accumulation of lipid may in some way reflect the intracellular energy turn-over. Alternatively, if the filtration theory (FRENCH, 1964; OSBORN, 1963; GOFMAN & YOUNG, 1963) of aortic lipid deposition is correct, then the accumulation of lipid at these points may be incidental to the fact that the supportive structures apparently provide compensatory tension at points of maximum arterial trauma (TEXON, 1963). Such traumatic forces may be due to direct haemodynamic pressures (GAUER & THRON, 1965) or to indirect physical pressure due to movements of neighbouring organs: e. g. of the cardiac muscle during systole and diastole in the case of coronary arteries (OSBORN, 1963; FINLAYSON, 1965).

The detailed structure of the arterial supportive thickenings in the hippopotamus and the elephant is illustrated in Fig. 1-3.

In very elderly buffalo and elephant, the dorsal crescentic fibrous band (apparently a compensatory arrangement for tensions set up at the bifurcation, where the intraarterial blood-pressure is stepped up as the blood enters the common iliac arteries and subsequent branches with reduced diameters) was found to accumulate calcific deposits in the *tunica media*. The onset and character of calcific deposition in this region may be directly associated with the ageing process, for where it occurred, it appeared to be unrelated to the general pattern of the pathogenesis of *medial sclerosis* (characterised by the progressive deposition of calcific deposits in the arterial *tunica media*) found in elephant in a degenerate habitat. In one declining and very elderly elephant, and one elderly buffalo, the calcific deposits in this crescentic band had formed a curved rod of organised bone.

Summary

During a field survey of cardiovascular disease in free-living wild animals in East Africa, a consistent technique was used for the study of both the normal internal anatomy and also diseases of the aorta and other arteries. As a result of the use of this technique it was possible to make a comparative study of the normal internal anatomy of the aorta of 43 species of manimals. Some peculiarities of anatomy of the arterial supportive structures of the klipspringer, gerenuk and hippopotamus were noticed, suggesting a functional specialisation suited to the circulatory requirements of these species in relation to their natural habits. Further specialisation was also noted in the arrangement of the branch arteries of the aorta.

As a result of these observations, described in this paper, it is suggested that the supportive structures found in the arterial walls of mammals, associated with the ostia of branches and bifurcations, function not only as passive supportive structures, withstanding and compensating high haemodynamic pressures operating at these points, but also actually controlling the amount of blood entering the branch arteries at any given time. The almost universal occurrence in mammals of intimal deposits of sudanophilic lipid at these points, unaccompanied by pathological reactions of the neighbouring tissues, is thought to represent a normal, physiological process. In the klipspringer (rupicolous) and the hippopotamus (amphibious), some of these supportive structures are anatomically so complex that it is difficult to regard them merely as some kind of vestigeal apparatur or as passive structural elaborations.

Zusammenfassung

Während eines Feld-Projektes, das sich mit der Erforschung von Kreislauf-Krankheiten in freilebenden, wilden Tieren in Ost-Afrika befaßte, wurde eine Standard-Technik ausgearbeitet, um sowohl die normale interne Anatomie der Aorta und der Hauptarterien, sowie auch deren Erkrankungen, zu untersuchen. Die konsequente Anwendung dieser Technik ergab die Möglichkeit einer vergleichsweisen Untersuchung der normalen internen Anatomie der Hauptschlagader in 43 Spezies von Säugetieren. Während dieser Untersuchung wurden einige anatomische Spezialisierungen in bezug auf die arterielle interne Verstärkungs-Struktur bei Klippspringer, Gerenuk (Giraffengazelle) und Flußpferd beobachtet. Diese lassen eine spezielle Funktion vermuten, die den besonderen Anforderungen des Kreislaufs dieser Tiere, bedingt durch ihre natürliche Lebensweise, angepaßt sein dürfte. Eine weitere Spezialisierung in der Anordnung der Zweig-Arterien wurde ebenfalls beobachtet.

Infolge der hier beschriebenen Untersuchungen wird vorgeschlagen, daß man die Verstärkungs-Strukturen in der Innenwand der Arterien von Säugetieren, die im engsten Zusammenhang mit den Ostien der Zweigarterien sowie mit den Gabelungen der Aorta stehen, nicht nur als passive Verstärkungs-Strukturen ansehen sollte, die dem besonderen haemodynamischen Druck an diesen Punkten Widerstand und Ausgleich leisten müssen, sondern daß diese Verstärkungs-Strukturen positiv den Zufluß des Blutes zu den Zweigarterien zu jeder gegebenen Zeit regulieren können. Das fast universelle Vorkommen von sudanophilen Fett-Ablagerungen in der *Tunika interna* der Aorta von Säugetieren an diesen Punkten, das nicht von pathologischen Reaktionen des umgebenden Gewebes begleitet ist, wird dementsprechend als ein normaler physiologischer Prozeß angesehen.

Bei Klippspringer (*rupicolous*) und Nilpferd (*amphibious*) sind diese Strukturen anatomisch so komplex, daß es schwer fällt, sie nur als eine Art Überbleibsel oder als passive strukturelle Elaborationen anzusehen.

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References

- BERTELSEN, S. (1963): The role of ground substance, collagen and elastic fibers in the genesis of atherosclerosis. In: Atherosclerosis and its Origin. (Eds.: M. SANDLER & G. H. BOURNE). New York: Academic Press.
- BOYD, G. S. (1963): The thyroid, iodothyronins and atherosclerosis. J. Atheroscler. Res. 1:26.
- BRANWOOD, A. W. (1963): Modern Concepts of the Pathogenesis of Coronary Atherosclerosis. Edinburgh: Livingstone.
- BUCK, R. C. (1963): Histogenesis and morphology of arterial tissue. p. 1-38. In: Atherosclerosis and its Origin. (Eds.: M. SANDLER & G. H. BOURNE). New York: Academic Press. CONTI, VON G. (1953): Über das Vorkommen von Sperrvorrichtungen in Arterien mit speziel-ler Berücksichtigung der "gestielten Polster". Acta Anat. 18: 234–255. COUTURIER, M. A. J. (1938): Le Chamois, *Rupicapra rupicapra*. Grenoble.

- FINLAYSON, R. (1965): Spontaneous arterial disease in exotic animals. J. Zool. Lond. 147: 239-343.
- FRECHKOP, S. (1955): Super-ordre des Ongulées. In Traité de Zoologie. (Ed.: P. P. GRASSÉ). 17. Paris: Masson et Cie.
- FRENCH, J. E. (1964): Atherosclerosis. In: General Pathology, 418-446. (Ed.: H. FLOREY). London: Llovd-Luke.
- GAUER, O. H., and THRON, H. L. (1965): Ch. 67. In: Handbook of Physiology. Sect. 2: Circulation. (Eds.: D. B. DILL, E. F. ADOLPH & C. G. WILBER). Washington: Am. Physiol. Soc.
- GILLMAN, T. (1964): A plea for arterial biology as a basis for understanding arterial disease. 2-23. In: Biological Aspects of Occlusive Vascular Disease. (Eds.: D. G.: CHALMERS & G. A. GRESHAM). London: Camb. Univ. Press.
- GOFMAN, J. W., and YOUNG, W. (1963): The filtration concept of atherosclerosis and serum lipids in the diagnosis of atherosclerosis. In: Atherosclerosis and its Origin. (Eds.: M. SAND-LER & G. H. BOURNE), 197-229. New York: Academic Press.
- GONZALEZ, I. E. (1963): Enzyme defects in the diseased arterial wall. p. 151-163. In: Evolution of the Atherosclerotic Plaque. (Ed.: R. J. JONES). Chicago: Univ. Press.
- GRASSÉ, P. P. (1955): (Ed.) Traité de Zoologie 17: p. 645.
- GRATIOLET, M. P. (1860): Recherches sur le système vasculaire sanguin de l'Hippototame. C. r. hebd. Séanc. Acad. Sci., Paris 51: 524-528.
- HOLMAN, R. L., McGILL, H. C., STRONG, J. P., and GEER, J. C. (1958): Natural history of atherosclerosis. Am. J. Path. 34: 209.
- KATZ, L. N., and PICK, R. (1963): Reversibility of the atherosclerotic lesion. In: Evolution of the Atherosclerotic Plaque. (Ed.: R. J. JONES). Chicago: Univ. Press.
- LIKAR, L. J., LIKAR, I. N., and ROBINSON, R. W. (1965): Levels of acid mucopolysaccharides of the bovine aorta at different stages of the sexual cycle. J. Atheroscler. Res. 5: 388-396.
- LYDDEKER, R. (1926): The Game Animals of Africa. London: Roland Ward, pp. 154-157.
- MCGILL, H. C., and GEER, J. C. (1963): The human lesion, fine structure. In: Evolution of the Atherosclerotic Plaque. (Ed.: R. J. JONES) Chicago: Univ. Press.
- OGILVIE, R. F. (1962): Histopathology. Edinburgh: Livingstone.
- OSBORN, G. R. (1963): The Incubation Period of Coronary Thrombosis. London: Butterworth.
- ROBERTS, J. C., and STRAUS, R. (Eds.) (1964): Comparative Atherosclerosis. New York: Harper & Row.
- SANDLER, M., and BOURNE, G. H. (Eds.) (1963): Atherosclerosis and its Origin. New York and London: Academic Press.
- SCHOLANDER, P. F. (1965): Animals in aquatic environment. Sect. 4. In: Handbook of Physiology. (Eds.: D. B. DILL, E. F. ADOLPH & C. G. WILBER) Washington: Am. Physiol. Soc.
- SCHOMBER, H. W. (1966): Die Giraffen- und Lamagazelle. No. 358, Neue Brehm-Bücherei. Ziemsen Verl. Wittenberg.
- SCLATER, P. L., and THOMAS, O. (1894–1900): The Book of Antelopes, 2.
- SIKES, S. K. (1966): The African elephant, Loxodonta africana: a field method for the estimation of age. J. Zool. Lond. 150: 279-295.
- (in press [a]): Observations on the ecology of arterial disease in the African elephant (Loxodonia africana) in Kenya and Uganda. (Zool. Soc. Lond. Symposium Nr. 21; Ed.: M. A. CRAWFORD). London: Academic Press.
- (in press [b]): The disturbed habitat and its effect on the health of animat populations, with especial reference to elephants. Proc. Roy. Soc. Med., (Sect. Comp. Med. Symp. "Controlling Mechanisms in Natural Populations in Relation to Human and Animal Medicine".)
- (1967): A survey of Cardiovascular disease in free-living wild mammals and birds with particular reference to the African elephant, *Loxodonta africana*. Thesis. London.
- SMITH, E. B., EVANS, P. H., and DOWNHAM, M. D. (1967): Lipid in the aortie intima: the correlation of morphological and chemical characteristics. J. Atheroscler. Res. 7: 171-186.

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SODEMAN, W. A. (Ed.) (1961): Pathologic Physiology, Mechanisms of Disease. Philadelphia:

STEHBENS, W. E. (1960): Focal intimal proliferation in the cerebral arteries. Am. J. Path. 36: 289-295.

TEXON, M. (1963): The role of vascular dynamics in the development of atherosclerosis, 167-159. In Atherosclerosis and its Origin. (Eds.: M. SANDLER & G. H. BOURNE). New York: Academic Press.

THORP, J. M. (1963): Effects of seasonal variation on lipid metabolism in animal and man, 169. In: The Control of Lipid Metabolism. (Ed.: J. K. GRANT). London: Academic Press.

THURLBECK, W. M. (1965): Arteriosclerosis in hippopotami. In: Comparative Atherosclerosis. (Eds.: J. C. Roberts & R. Straus). New York: Harper & Row.

VERHEYEN, R. (1954): Monographie éthologique de l'hippopotame (Hippopotamus amphibius Linné). Bruxelles: Inst. Parcs Nat. Congo Belge.

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Notiz über einen Bastard zwischen Arctocephalus pusillus (Schreber, 1776) und Zalophus californianus (Lesson, 1828)

Von HARALD SCHLIEMANN

Eingang des Ms. 19. 6. 1967

Im Tierpark Hagenbeck wurde am 8. Juni 1966 von einem Zalophus californianus Qein weibliches Jungtier¹ geworfen, als dessen väterlicher Elter nur ein Arctocephalus pusillus \mathcal{S} in Betracht kommt. Die Geburt erfolgte am Tage vor den Augen des Publikums. Der unmittelbar nach der Geburt herbeigerufene Wärter gab an, das Tier sei sofort tot gewesen.

In der Literatur (JENNISON, 1914; LÖNNBERG, 1929; GRAY, 1954 u. a.) finden sich Angaben über vier Pinnipedier-Bastarde, die - wie meistens in solchen Fällen - in Zoologischen Gärten zur Beobachtung gelangten. JENNISON berichtet von drei Tieren, die ebenfalls von einem Seebären (3)-Seelöwen (2)-Paar stammten und in den Jahren 1911, 1912 und 1913 in Belle Vue Gardens in Manchester geboren wurden. Während der erste Bastard tot aufgefunden wurde und der zweite nur einen Tag lang lebte, konnte der dritte erfolgreich aufgezogen werden. Er lebte noch zum Zeitpunkt von JENNISONS Berichterstattung, d. h. ein Dreivierteljahr nach seiner Geburt. Von den beiden ersten Tieren sind keine näheren Einzelheiten bekannt, von dem dritten, einem Männchen, werden Entwicklung und einige seiner Gewohnheiten geschildert. Dieser Bastard soll im Aussehen seinem Arctocephalus-Vater sehr geähnelt haben. Über das weitere Schicksal dieses Tieres ist leider nichts bekannt. LÖNNBERG beschreibt unter Beifügung von Abbildungen einen Mischling zwischen Halichoerus grypus & und Phoca hispida Q, der 1929 im Stockholmer Zoo offensichtlich bald nach seiner Geburt tot aufgefunden wurde. Das Studium des Schädels zeigte, daß dieser Bastard trotz Übereinstimmung mit der Kegelrobbe im wesentlichen dem mütterlichen Tier glich.

Verpaarungen von Individuen, die verschiedenen Säugerarten oder -gattungen angehören, sind aus Zoologischen Gärten in größerer Zahl beschrieben worden (GRAY, 1954). Angehörige verschiedener Arten üben unter natürlichen Bedingungen normaler-

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